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ORIGINAL ARTICLE

T. M. Brown-Brandl · R. A. Eigenberg · G. L. Hahn · J. A. Nienaber · T. L. Mader · D. E. Spiers · A. M. Parkhurst

Analyses of thermoregulatory responses of feeder cattle exposed to simulated heat waves

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Abstract Heat stress in feedlot cattle causes reduced performance, and in the most severe cases, death of the animals, thus causing the loss of millions of dollars in revenue to the cattle industry. A study was designed to evaluate dynamics of thermoregulation and feeding activities when feeder cattle were exposed to simulated heat waves, in comparison with repeated sinusoidal hot and thermoneutral environments. Nine beef steers were randomly assigned to an individual pen in one of three environmental chambers. Each chamber was subjected to each of three temperature regimes (Heatwave simulation from Rockport, Mo., 1995, Heatwave simulation from Columbia, Mo., 1999, and Controlled heat stress treatment of 32±7°C) for a period of 18 days, according to a Latin square treatment design, with a 10-day thermoneutral period (18±7°C) separating treatment periods. Respiration rate, core body temperature, heat production, feed intake, and feeding behavior were measured on each animal for the duration of the experiment. Differences were found in all treatments for all parameters except feeding behavior. It was shown that the two simulated heat waves elicited very different thermoregulatory responses. Based on these results the heat wave centered at Rockport, Mo. in 1995 was devastating because the animals were not acclimated to hot conditions, thus causing an acute response to heat stress. The responses of cattle to conditions at Columbia, Mo. showed some acclimation to heat prior to the peak stress days, and therefore a dampened response was seen. It appears the extreme conditions at Columbia, Mo., 1999 were made severe by environmental conditions not simulated during this study (low wind speed and intensive solar radiation). Overall, it was determined while a cyclic heat stress treatment is a representative model to test heat stress in cattle, further heat stress experiments should be conducted in an actual feedlot.

Keywords Heat stress · Bioenergetics · Body temperature · Feed intake · Respiration rate

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T. M. Brown-Brandl (✉) · R. A. Eigenberg · G. L. Hahn · J. A. Nienaber
USDA-ARS,
U.S. Meat Animal Research Center,
Clay Center, NE, USA
e-mail: brandl@email.marc.usda.gov
Tel.: +1-402-7624279
Fax: +1-402-7624273

T. L. Mader
University of Nebraska,
Concord, NE, USA

D. E. Spiers
University of Missouri,
Columbia, MO, USA

A. M. Parkhurst
University of Nebraska,
Lincoln, NE, USA

Introduction

Hot weather affects animal bioenergetics, and has negative impacts on animal performance and well-being. Reductions in feed intake, growth, and efficiency are commonly reported in heat stressed cattle (Hahn 1985). The impact of heat load on these production losses are quite varied, ranging from little to no effect in a brief exposure, to death in vulnerable animals during an extreme event (Hahn and Mader 1997).

Heat waves are a recurring phenomenon in cattle-producing areas of the USA. A heat wave is defined as “a period of abnormally uncomfortable hot and usually humid weather of at least 1 day duration, but conventionally lasting several days to several weeks ...” (AMS 1989). Hahn and Mader (1997) reported an operational definition of heat waves as “3–5 successive days with maximum temperatures above a threshold, such as 32°C.” Several heat waves have occurred in the Midwest in the last 10

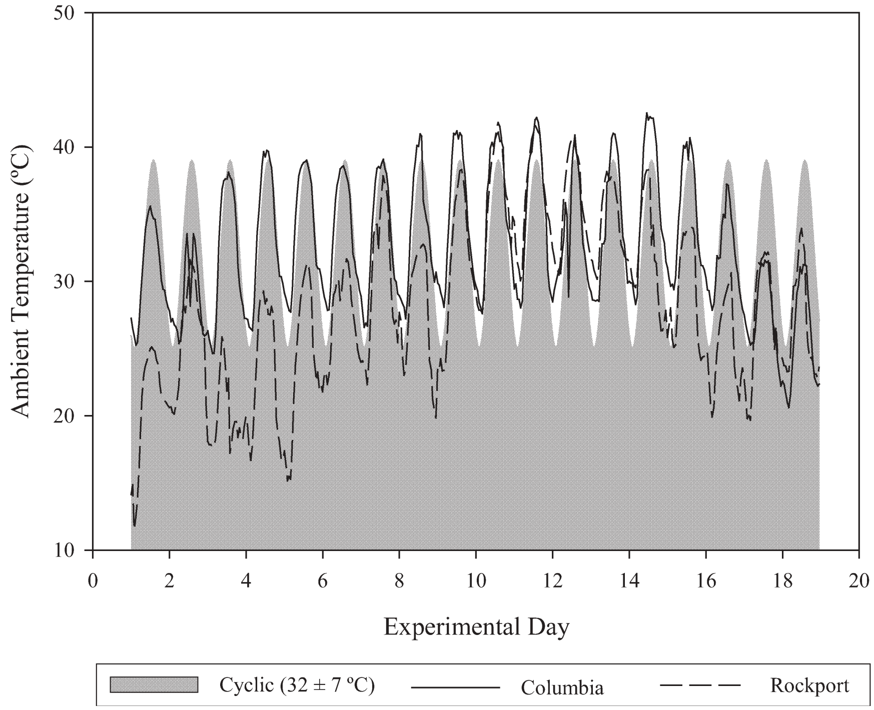


Fig. 1 A comparison of ambient temperature in the three temperature treatments: Cyclic (32±7°C); Columbia (conditions at Columbia, Mo., July 1999); Rockport (conditions at Rockport, Mo., July 1995)

years causing the death of thousands of feedlot cattle (Hahn 1999), and loss of millions of dollars in revenue to the cattle industry in direct cattle losses and indirect performance losses.

One devastating heat wave occurred 11–12 July 1995 killing an estimated 3,750 head of cattle in a 13-county area of western Iowa. Direct losses were estimated at $2.8 million and production losses were estimated at $28 million (USD) (Busby and Loy 1996). Hungerford et al. (2000) reported on a heat wave in eastern Nebraska in July 1999. More than 5,000 head of cattle died due to excessive heat load over this 2-day period (20–21 July); losses totaled between $21.5 and $35 million. In both of these cases, high temperature and solar radiation were combined with high humidity and low wind speed to create a high stress situation. Both of these studies reported on potential risk factors based on mortality data collected from producer surveys. The results indicate dark hides, lack of shade, west-facing pens, lack of adequate space or water flow rate at the waterer were determined as risk factors. While the results of these studies are important and give an interesting view of severely stressed animals not repeatable in controlled experiments, the data is only observational, and does not provide any information on the metabolic state of the animals during the peak heat stress.

Typically, heat stress studies rely upon a high constant (i.e., 32°C) or a cyclic temperature (i.e., 32±7°C) to simulate the weather that would induce heat stress in the field. However, heat waves do not have uniform temperatures from day to day, and the nighttime low has been found to directly impact the level of stress imposed on the animal (Hahn and Mader 1997). A study was designed to test a Cyclic condition (32±7°C) against two known severe heat waves (one that occurred in 1995 at Rockport, Mo. and the other in 1999 at Columbia, Mo.) to investigate bioenergetic responses of the cattle exposed to each set of conditions.

Materials and methods

Nine crossbred steers (1/4 Angus, 1/4 Hereford, 1/4 Pinzgauer, 1/4 Red Poll), in a summer coat condition, weighed 400.3±10.0 kg and were an average age of 452±5.1 days. Steers were randomly assigned to individual stalls in one of three environmentally controlled chambers (three animals per chamber). This crossbreed was selected for the experiment because it mimics crossbreed steers commonly seen in feedlots across the Midwest. The animals were given an 8-day acclimation period to adjust to laboratory surroundings, procedures, equipment, and thermoneutral environmental conditions [ambient temperature (t_a) of 18±7°C and a dew point temperature (t_{dp}) of 7°C]. A 14 h:10 h controlled photoperiod was selected with lights on from 0630 to 2030 hours. A standard feedlot ration (high moisture corn plus silage, average dry matter of 63.6±0.5%, average nitrogen content of 2.0±0.1%, average ash content of 5.0±0.3%, and average gross energy of 4,362±13 kcal/kg) was fed ad libitum, with fresh feed provided daily. Daily refusals were removed and weighed throughout the experiment. Steers were provided with free access to water and a salt block.

Each chamber was subjected to each of three temperature treatments: (1) Cyclic (t_a=32±7°C); (2) conditions at Columbia, Mo. during July and August 1999; (3) conditions at Rockport, Mo. during July 1995 (Fig. 1). In all heat-stress treatments t_{dp} was held constant at 14°C. A Latin square treatment design was used, with all animals exposed to every treatment over three separate periods. The duration of each treatment period was 18 days, with a minimum of a 10-day thermoneutral period (t_a=18±7°C; t_{dp}=7°C) separating the treatment periods. During the thermoneutral period, ambient air temperature cycled on a 24-h basis, with maximum occurring at 1330 hours and minimum occurring at 0130 hours. Animals were exercised and weighed prior to the beginning and after the end of every treatment period. Feed samples were collected throughout the treatment periods and analyzed for dry matter, ash, nitrogen, and gross energy.

Respiration rate (RR), core body temperature (t_{core}), heat production (HP), and feeder weights were continuously recorded during the imposed treatment and thermoneutral periods. Respiration rate was obtained from all animals using respiration rate monitors; the output signal from the RR sensor was recorded for 1 min every 15 min at 10 Hz (Eigenberg et al. 2000). These data were then post-processed using in-house developed software (Eigenberg et al. 2000).

Core body temperature was measured using a telemetry system manufactured by HQ (West Palmetto, Fla., USA). Prior to the experiment, a licensed veterinarian implanted a transmitter in the abdominal cavity of each steer (Brown-Brandl et al. 2003a). Data were logged on a CorTemp logger at a frequency of one reading every minute. Rectal temperature was used as a backup measurement of t_{core}. Rectal temperature was measured using a YSI (Yellow Springs, Ohio, USA) stainless steel probe inserted to a depth of approximately 20 cm and recorded each minute on a Pace Scientific, Pocket Logger (Charlotte, N.C., USA). Rectal temperatures were converted to t_{core} by an equation, which was developed for each animal from data that was collected from both systems simultaneously.

Total heat production was calculated using indirect calorimetry methods. Each of the environmental chambers containing three animals was used as a calorimeter chamber. Inlet airflow was measured using an electronic differential pressure transmitter, which was fitted inside the inlet air duct. The error in flow measurement was less than 2.5%. Calorimeter gas samples were analyzed for O_2, CO_2, and CH_4 once every 15 min. Oxygen and CO_2 were measured to the nearest 100 ppm, while CH_4 was measured within 10 ppm. Total heat production was calculated using the total inlet air added, and the average concentrations of O_2, CO_2, and CH_4 over a 24-h period for fresh inlet air and chamber air.

Feeder weights were determined using a load cell (Model 1250, Tedea-Huntleigh International, Israel) placed under the feedbox. Weights were read and stored each minute using a data acquisition system (Iotech., Cleveland, Ohio, USA), and software developed in-house. From these data, feeding behavior parameters [daily feed intake (FI), total daily eating duration, meal size, meal duration, and frequency of meals] were calculated.

Daily averages of t_{core}, RR, FI, HP and feeding behavior parameters were analyzed using repeated measures in a linear mixed effects model, with a first-order autoregressive order-one error structure (SAS 1999; Littell et al. 1996). The model included chamber, period, and animal nested within chamber and period as random effects, and treatment (TRT), day of exposure (DAY), and TRT × DAY interaction as fixed effects. Response differences were considered to be significant when the probabilities were less than 0.05.

Temperature impacts on daily average t_{core}, RR, FI, and HP were analyzed using the general linear fixed effects model procedure, looking for effects of average daily ambient temperature (linear and quadratic terms) and animal. The regression procedure was used to develop an equation to relate t_{core}, RR, and FI to temperature; terms in the model statement were dependant on the outcome of the results from the general linear fixed effects model procedure (SAS 2000).

The lag or offset between RR and temperature was determined using average 15-min data (all animals averaged). Daily lags for both the heat stress and thermoneutral periods were determined by generating regression equations for each offset (15, 30, 45 min, etc.), then maximizing the coefficient of determination (R^2) using the SLOPE and RSQ functions in Microsoft Excel. Differences between heat stress and thermoneutral lags were determined with a one-tailed t-test, assuming unequal variances using the data analysis tools in Microsoft Excel. A similar procedure was used to generate lags between t_{core} and temperature on a daily basis for all treatments.

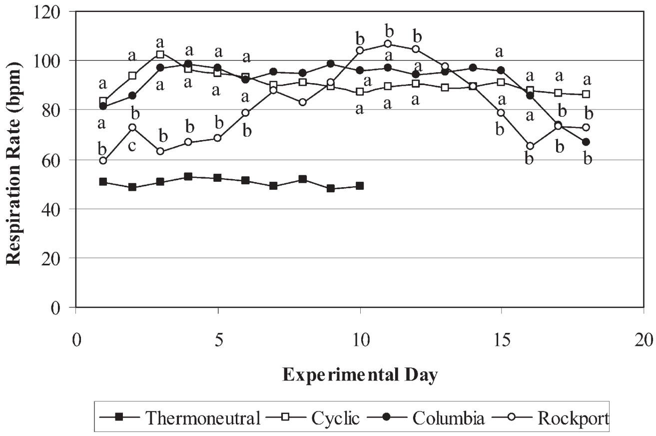


Fig. 2 Treatment differences in average respiration rate for each day through the treatment period. Points with different letters are significantly different (P<0.05). Thermoneutral responses are added only for visual comparison, and were not statistically compared

Results

The average steer weights during periods I, II and III were 403.8±10.3, 421.9±12.0, 447.7±11.9 kg, respectively. The actual chamber temperature followed the protocol temperatures well. It appears that in all treatments on most experimental days, ambient temperatures overshot set point maximums. This small overshoot in temperature resulted in the average error being positive. The Columbia treatment had the largest error—average temperature was 0.8°C higher than the set point, while Rockport and Cyclic treatments averaged 0.6°C higher than the set point.

When ambient temperature of two simulated heat wave treatments and Cyclic (32±7°C) treatment were compared, differences in patterns emerged (Fig. 1). The Columbia treatment is similar to the Cyclic treatment, except for higher nighttime lows and a slight increase in average temperature through most of the 18-day period. In comparison, Rockport treatment had a steep rise in temperature, with just a few days of extreme temperature, and little to no nighttime recovery, followed by a gradual reduction in temperature. The Rockport treatment was cooler than the Columbia treatment on all days except days 10, 11, and 12, when the two were nearly identical.

Respiration rate

The statistical analysis that used the mixed procedure revealed first-order autoregressive and residual terms to be significant, as well as the fixed effects of treatment, day, and treatment by day.

When comparing RR between Columbia and Cyclic treatments, only days 2, 17, and 18 were significantly different (Fig. 2). All these days very clearly show the Columbia temperature to be lower, which in turn lowered RR. On days 7–15, Columbia treatment animals had a slightly higher RR than the Cyclic, although not signifi-

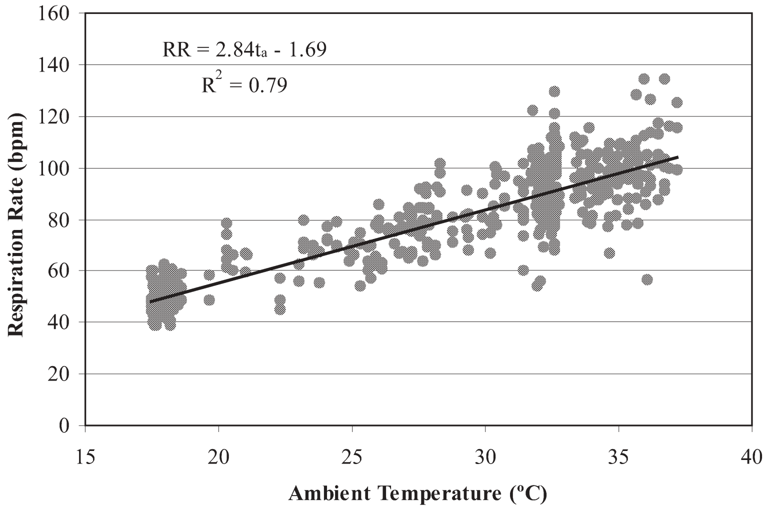


Fig. 3 The effects of ambient temperature on respiration rate of crossbred cattle exposed to cyclic thermoneutral and heat-stress conditions (including simulated heat waves) in an environmental chamber

cant. During days 8–11, and 13 and 14, the Columbia treatment had a higher maximum and minimum temperature, which resulted in a numerically higher RR. On days 7, 12, and 15 the maximum temperatures in both treatments were very similar, but the minimum temperatures were higher in the Columbia treatment, which resulted in a numerically increased RR.

Because the temperature pattern in the Rockport treatment was very different from either of the other two temperature treatments, the pattern in RR data throughout the 18-day period was also very different (Fig. 2). Respiration rate during the Rockport treatment was significantly different from the other two treatments on days 1–6, 10–12, and 15 and 16, and significantly different from the Cyclic treatment on days 17 and 18. During days 1–6 and 15–17 the temperature in the Rockport treatment was lower than the Cyclic treatment, resulting in a significantly lower RR. On days 10–12 the Rockport treatment had higher maximum and minimum temperatures than the Cyclic treatment, resulting in significantly higher RR responses. The RR was also significantly higher in the Rockport treatment compared to the Columbia treatment on the same days (days 10–12).

The general linear model procedure found that RR had a significant animal and linear temperature effect. Statistical analysis confirms this high correlation between RR and average temperature. A simple regression analysis revealed 79% of the variation associated with RR was accounted for by temperature (Fig. 3). Adding animal to the model only increased the R^2 to 0.83, thus animal accounted for an additional 4% variation, leaving only 16% unaccounted.

It was found that the lag between response in RR and the change in temperature was 1.8±0.12 h, and varied between 0 and 4.5 h. There was no significant difference (P=0.085) between the average lag for the heat stress treatments (1.86±0.13 h) and thermoneutral treatment (1.45±0.25 h). Figure 4 illustrates the daily lag changes during three heat-stress treatments and thermoneutral conditions. The Cyclic condition elicited a fairly constant lag response between 2 and 3 h (mean of 2.49±0.13 h); day 3 and day 14 were the only exceptions, with lag times of 0.75 and 3.5 h, respectively. The Columbia (1.51±0.20 h) and Rockport (1.58±0.27 h) treatments had lags significantly lower and more variable than the Cyclic treatment (P<0.01). While the Columbia treatment elicited a fairly uniform response from day 2 to day 16, the animals exposed to the Rockport treatment experienced an increase in the lags on days 11–13. It was shown that lags in RR increased with increasing average daily temperature; a regression analysis, using data from only the simulated heat waves, indicated that temperature accounted for 44.4% of the variation in lag time.

Core body temperature

The statistical analysis generated from the mixed procedure revealed significant random effects of animal (chamber × period), first-order autoregressive term and residual term, and fixed effects of day and treatment by day.

When comparing t_{core} between treatments, only one significant difference emerged. On day 3, the animals exposed to Cyclic treatment had a significantly higher t_{core} than animals exposed to Rockport treatment. Because only 1 day was significant at the P<0.05 level, trends were added to the discussion (P<0.1) (Fig. 5).

The general linear model procedure found that t_{core} had a significant animal and linear temperature effect. Unlike RR, t_{core} appears to have many factors other than ambient temperature that affect it. A simple regression analysis revealed ambient temperature only accounted for 29% of total variation (Fig. 6). Adding animal to the model increased the R^2 to 0.59, thus animal accounted for an additional 30% of variation. However, using both animal and ambient temperature in the model still leaves 41% of total variation unaccounted.

The lag analysis revealed that the response in t_{core} lagged temperature by an average of 5.95±0.25 h, and

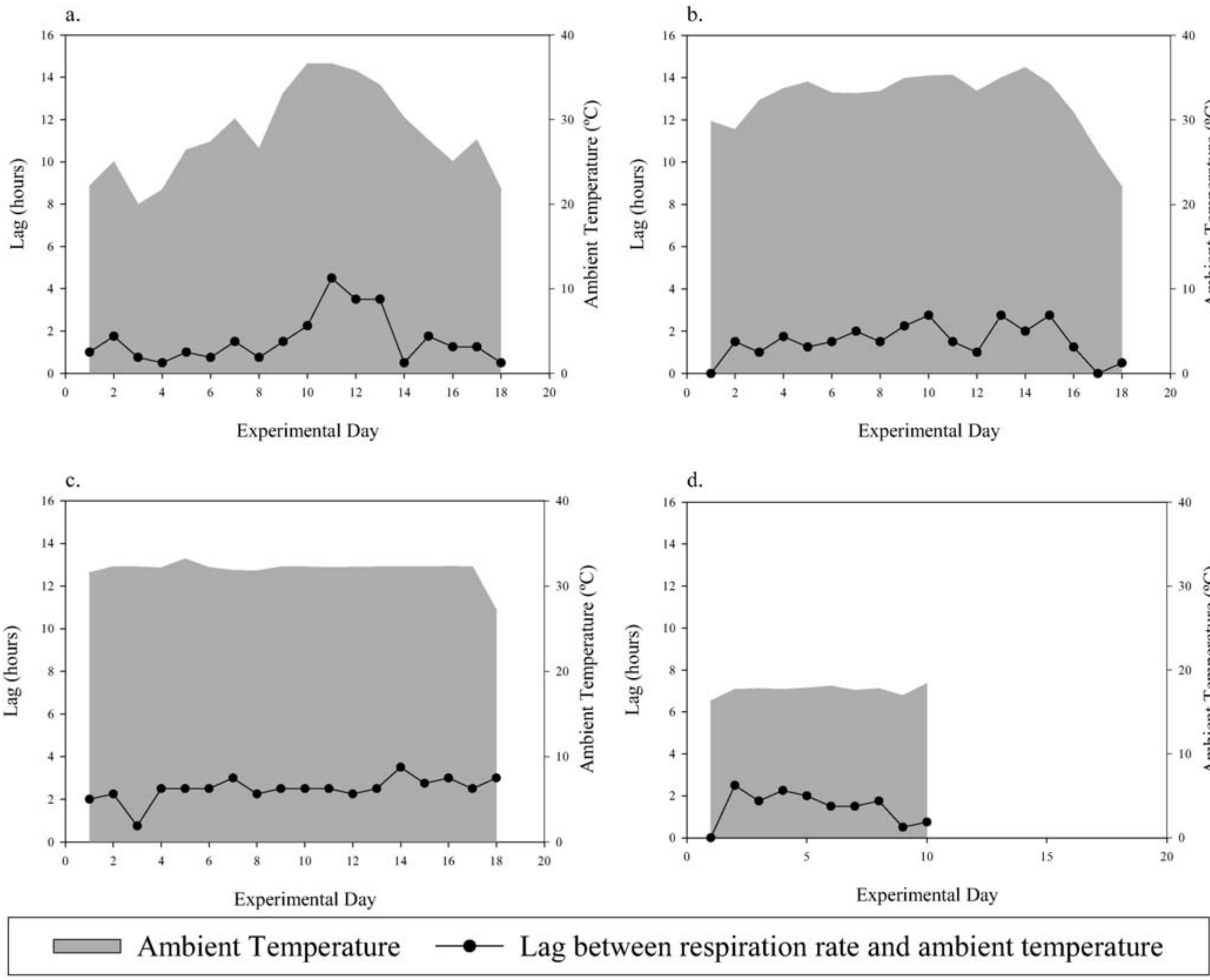


Fig. 4 Daily associated lags or offsets between respiration rate and ambient temperature for each of the three heat stress treatments and the thermoneutral period: **a** Rockport, Mo. (1995); **b** Columbia, Mo. (1999); **c** Cyclic treatment (32±7°C); **d** Thermoneutral period (18±7°C)

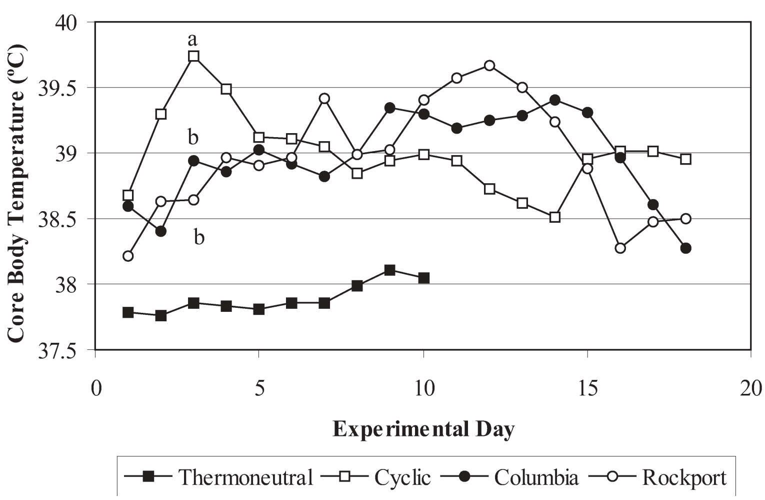


Fig. 5 Treatment differences in average core body temperature for each day through the treatment period. Points with different letters tended to be different ($P<0.05$). Thermoneutral responses are added only for visual comparison, and were not statistically compared

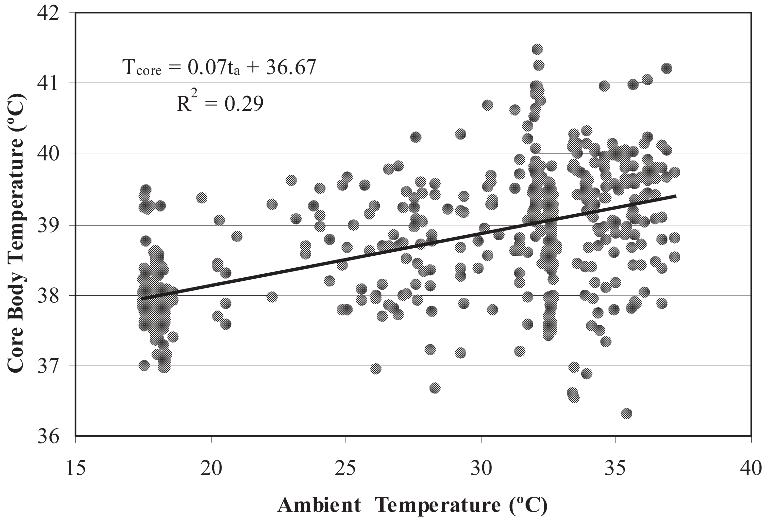


Fig. 6 The effects of ambient temperature on core body temperature of crossbred cattle exposed to cyclic thermoneutral and heat-stress conditions (including simulated heat waves) in an environmental chamber

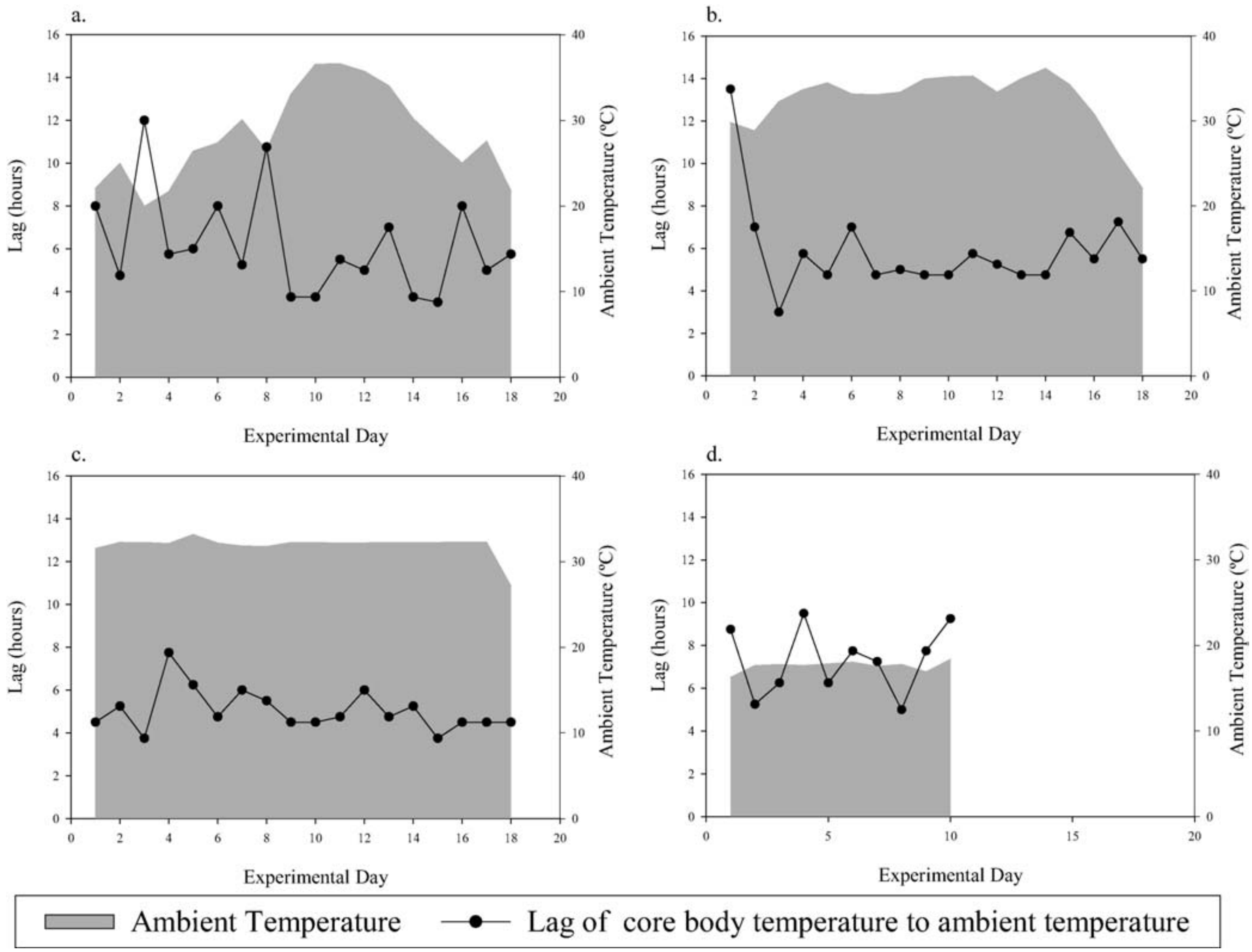


Fig. 7 Daily associated lags or offsets between core body temperature and ambient temperature for each of the three heat stress treatments and the thermoneutral period: **a** Rockport, Mo. (1995); **b** Columbia, Mo. (1999); **c** Cyclic treatment (32±7°C); **d** Thermoneutral period (18±7°C)

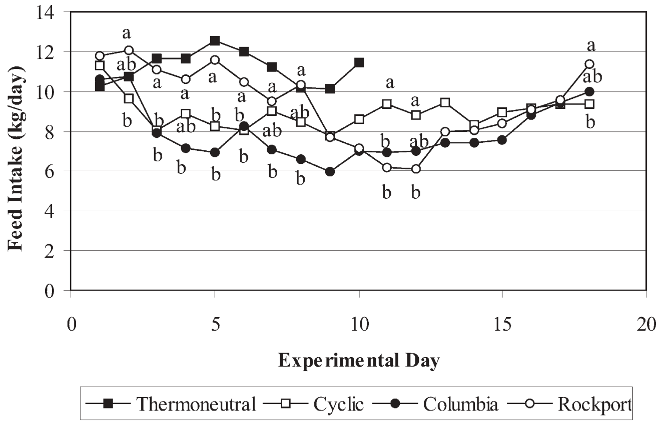


Fig. 8 Treatment differences in feed intake for each day throughout the treatment period. Points with different letters are significantly different (P<0.05). Thermoneutral responses are added only for visual comparison, and were not statistically compared

varied between 3 and 13.5 h (Fig. 7). Cattle exposed to thermoneutral conditions had a larger lag time in t_{core} (7.3±0.50 h) than cattle exposed to heat stress conditions (5.70±0.27 h, P=0.0007). The Cyclic treatment elicited a 5.04±0.23 h lag with a fairly uniform lag from day 6 to day 18. It appears there is a change in the animal's response between days 3 and 5, with first a decrease in the lag on day 3, then a large increase in lag on day 4. As with RR responses, the Cyclic treatment tended to effect the animal's response differently than the simulated heat waves. The Columbia treatment elicited a 5.9±0.51 h lag, which tended to be longer than the Cyclic treatment (P=0.076), while an average lag of 6.2±0.56 h was found in response to the Rockport temperature (P=0.035). The difference in lag response between the two simulated heat waves was not significant (P=0.34). The first day of the Columbia treatment resulted in a large lag in t_{core} response. Aside from the first 2 days of the Columbia treatment, lag in t_{core} remained reasonably constant, ranging from 3 to 7.5 h. The lag response to the Rockport treatment appeared to be very responsive to changes in temperature, with a slight decrease in temperature changing the lag up to 7.25 h; overall, the lag varied from 3.75 to 12 h. It was shown that lags in RR increase, with increasing average daily temperature; a regression analysis, using data from only the simulated heat waves, indicates that temperature describes only 17.7% of the variation.

Feed intake

The statistical analysis generated from the mixed procedure revealed significant random effects of animal (chamber × period), first-order autoregressive term and residual term, and fixed effects of day and treatment by day.

When comparing FI between Cyclic and Columbia treatments, FI was numerically lower on all days except day 1 and day 18, however, only days 11 and 12 were statistically significant. When comparing FI of the Columbia treatment with the Rockport treatment, FI was significantly lower in the Rockport treatment on days 2–7 and day 18 (Fig. 8).

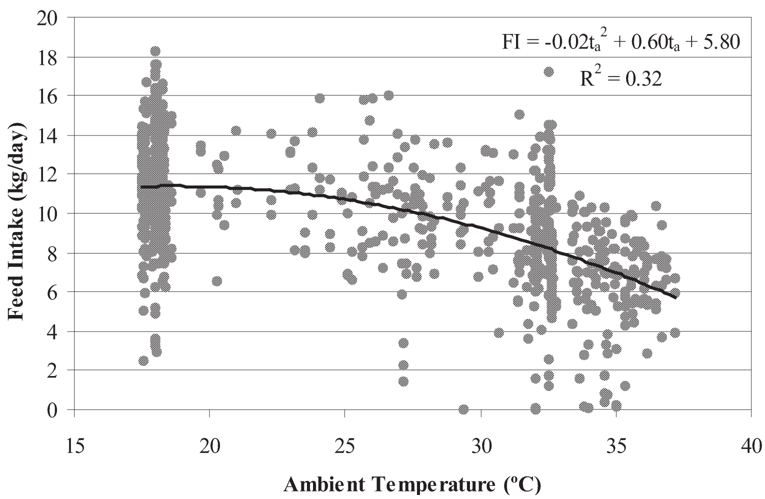
The general linear model procedure found that FI was significantly affected by animal, and linear and quadratic ambient temperature effects. Taking the first derivative of the equation developed from the regression procedure in SAS reveals a breakpoint of approximately 18.5°C.

Unlike RR and t_{core}, FI has a significant quadratic affect. The regression analysis revealed ambient temperature and ambient temperature squared account for 30% of the total variation (Fig. 9). Adding animal to the model increased the R^2 to 0.47, thus animal accounted for an additional 17% of the variation, leaving 53% of total variation unaccounted.

Feeding behavior

The parameters of number of meals, duration of eating, average meal duration, and average meal amount were analyzed. The statistical analysis generated from the

Fig. 9 The effects of ambient temperature on feed intake of crossbred cattle exposed to cyclic thermoneutral and heat-stress conditions (including simulated heat waves) in an environmental chamber



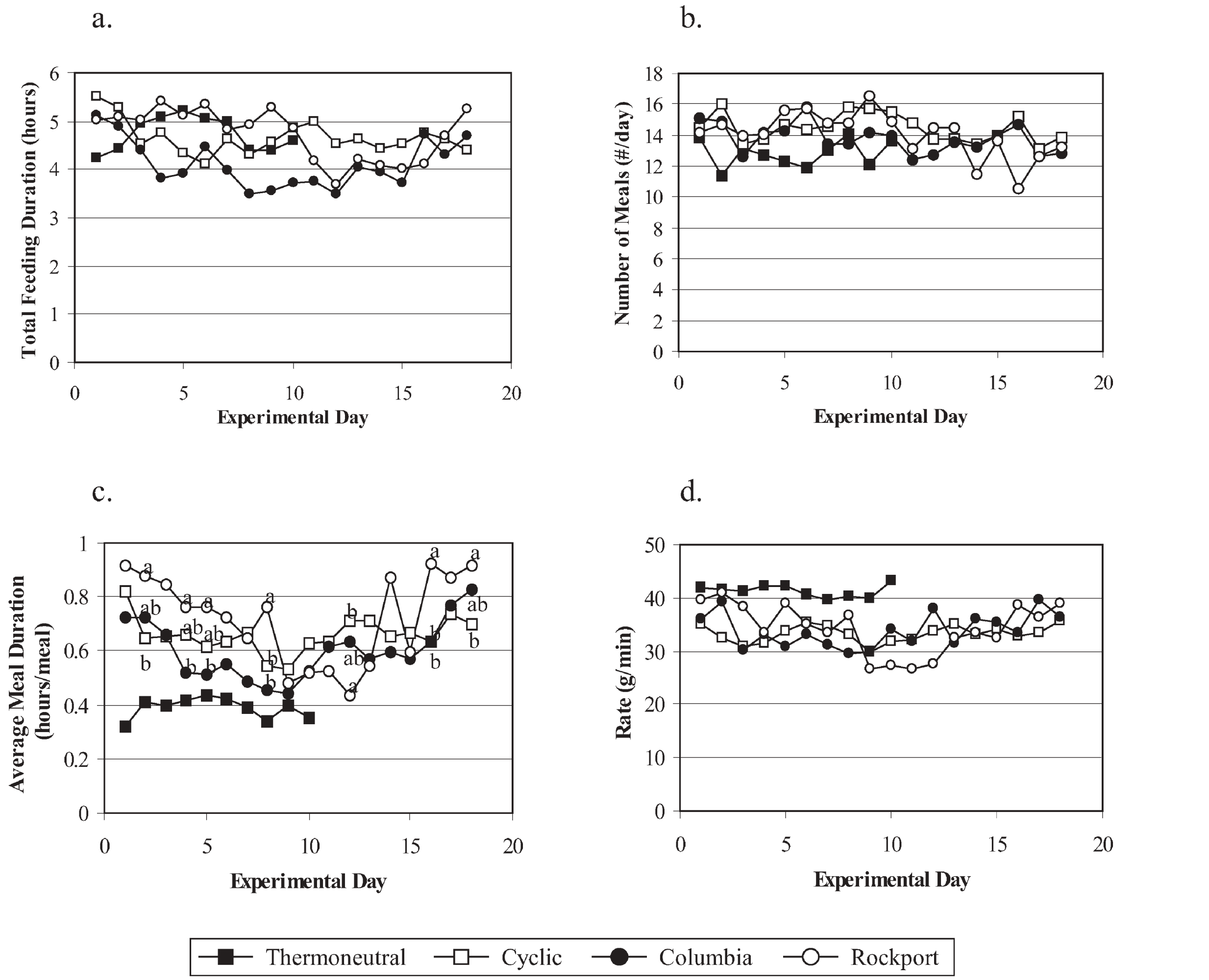


Fig. 10 Treatment differences in four feeding behavior parameters for each day throughout the treatment period: **a** total feeding duration per day; **b** number of meals per day; **c** average meal duration; **d** rate of eating. Points with different letters are significantly different ($P<0.05$). Thermoneutral responses are added only for visual comparison, and were not statistically compared

mixed procedure revealed significant random effects of animal (chamber × period), first-order autoregressive term, and residual term for all feeding behavior parameters. Duration and average meal duration had a significant day effect. The only feeding behavior parameters that were affected by treatment or treatment by day was rate and average meal amount that were significantly affected by day and treatment by day (Fig. 10).

Total heat production

The statistical analysis that utilized the mixed procedure revealed first-order autoregressive and residual terms to be significant ($P<0.05$), in addition to the fixed effect of day. The general linear model procedure found that HP had only a significant quadratic temperature effect.

It appeared that cattle exposed to Cyclic treatment acclimated to higher temperatures in 3–4 days. Although not shown in the graph, HP over the first 4 days were not significantly different from each other; days 1–3 were essentially different from days 2–16. Cattle exposed to Cyclic treatment had a slightly higher (although not significant) HP, compared to Columbia treatment throughout the treatment period. This suggested that nighttime low temperatures impact cattle more than daytime highs, as Cyclic treatment had similar or higher daytime but lower nighttime lows. Rockport had significantly higher HP on days 3–5, 8, and 9 than Cyclic treatments (Fig. 11). Rockport had lower temperatures (except for day 9), which allowed greater FI and thus increased HP.

While it appeared that exposure time played an important role in HP of the animal, average daily temperature appeared to drive FI, and thus HP. A simple regression analysis revealed 56% of variation associated with HP was accounted for by temperature (Fig. 12); because HP was measured on a chamber basis, no animal effect could be analyzed. The linear component of temperature only tended to have an impact on HP (P=0.11), and accounted for 21% of total variation, while quadratic temperature effect accounted for the other 79% of explained variation.

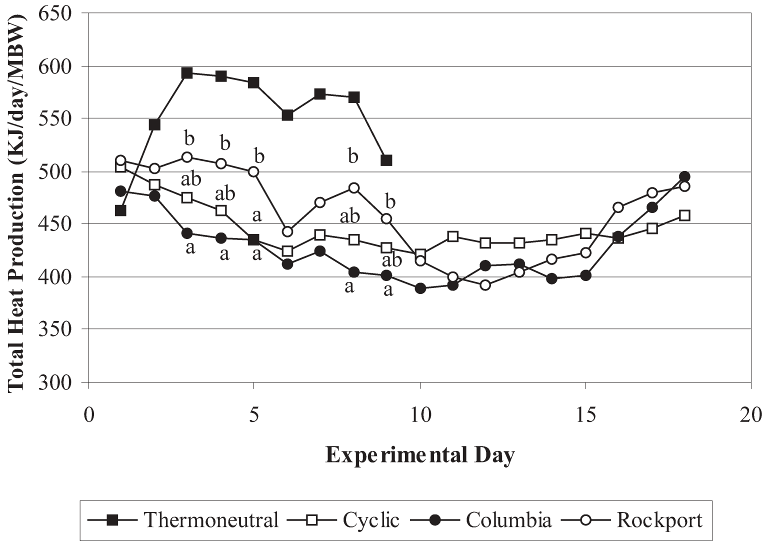


Fig. 11 Treatment differences in total heat production for each day throughout the treatment period. Points with different letters are significantly different ($P<0.05$). Thermoneutral responses are added only for visual comparison, and were not statistically compared

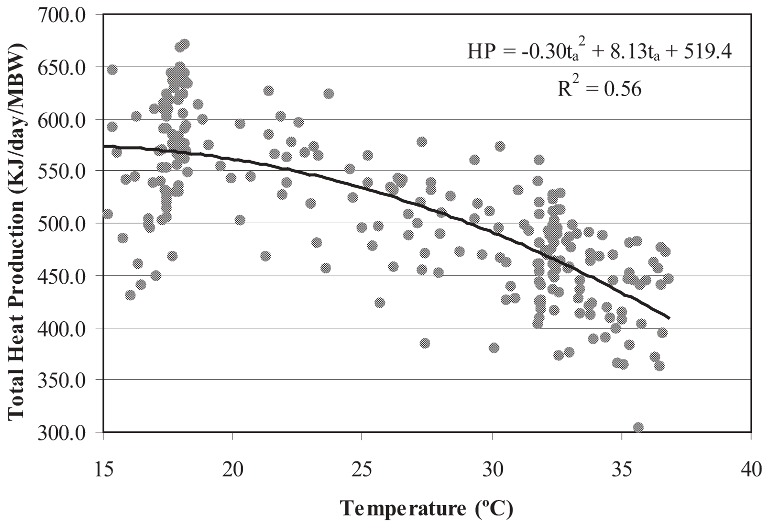


Fig. 12 The effects of ambient temperature on total heat production of crossbred cattle exposed to cyclic thermoneutral and heat-stress conditions (including simulated heat waves) in an environmental chamber

Discussion

The mixed procedure revealed the significance of the first-order autoregressive term in all parameters measured. The significance of the first-order autoregressive term simply means the current day's response is related to the previous day's, which is not surprising considering previously reported Green's function analysis indicating effects of hot conditions on current responses were impacted by temperatures for up to 60 h preceding (Hahn et al. 1987). Carry-over effect in HP is probably associated with the impact of FI and gut fill on HP. Since HP originates from breakdown and utilization of feedstuff, it is significantly impacted by FI (Brown-Brandl et al. 2003b; Close and Mount 1978) and gut fill.

Differences between daily responses in the mixed procedure analysis indicated some acclimation to the environment. When comparing the Cyclic treatment with the Columbia treatment, days 4, 5, and 6 were similar to days 7, 12, and 15 in that both treatments had similar maximum temperatures, while the Columbia treatment had a higher minimum temperature. Cattle RR response was similar in the two treatments. When comparing the two simulated heat waves, days 10–12 have a similar temperature pattern. However, different responses are found, where cattle's response to the Rockport treatment results in a higher RR. The difference in these responses could be explained by a difference in acclimation. The literature shows some mixed results on the effect of acclimation on RR. Kibler et al. (1949) showed a decrease in RR when cattle were acclimatized to temperature, while both Hahn et al. (1997) and Brown-Brandl et al. (2003b) reported no significant difference in RR between acute and chronic stress.

Upon visual inspection of data, it is very apparent that daily average temperature is not the sole driving force in t_{core}. Unlike RR, t_{core} responds to Columbia and Cyclic treatments very differently. The Cyclic treatment elicits a large peak in t_{core} over the first 4 days, then a gradual decrease from day 5 to 14, followed by a small increase over the last 4 days. The Columbia treatment caused only a gradual rise in t_{core} through day 15, and then a decrease. Changes in t_{core} in the Columbia treatment appear to be correlated with ambient temperature, where both t_{core} and ambient temperature gradually increased over the first 15 days, then both t_{core} and ambient temperature decreased. A similar response is observed in the Rockport treatment, where t_{core} tracks ambient temperature. In a comparison of Rockport and Columbia treatments (days 10–12), temperature patterns are very similar; however, t_{core} response in the Rockport treatment is 0.3°C higher. This provides some indication of acclimation in the Columbia treatment. Changes in t_{core} in the Cyclic treatment appear not to be correlated with temperature because of a strong acute/chronic component. It is interesting that both Cyclic and Rockport treatments elicit what could be called an acute response, while the Columbia treatment did not appear to have an acute response.

The response in FI in the Columbia treatment indicates FI is affected by higher daytime temperatures (days 8–5), and higher nighttime temperatures (days 2–7). Feeding behavior parameters measured in this paper indicate that under heat-stress conditions, these cattle slightly reduce number of meals, and duration of eating remain the same; rate of eating slow and average meal duration increase. This would suggest that animals in these situations cope with heat stress by slowing their rate of eating, which in turn reduces average meal amount. This does not agree with behavior of cattle in the feedlot; feedlot heifers under higher environmental temperatures decrease time spent eating compared to heifers exposed to thermoneutral conditions (Brown-Brandl et al. 2003c). However, during this study the water bowl was very close to the feed box, thus providing a constant encouragement to eat. This might have influence on the animals' feeding behavior.

The responses of the parameters to increasing temperature are described using a general linear model procedure. Surprisingly, no quadratic temperature effect is found in either the RR or t_{core} responses. Both Hahn et al. (1997) and Eigenberg et al. (2002) report the breakpoint in RR response between 20 and 25°C, while Hahn et al. (1992) and Leonard et al. (2001) report similar breakpoints in the t_{core}. It is possible that no quadratic effect is found in either parameter, because there are not sufficient data points between 18 and 25°C in the current study. Although a quadratic effect is found in FI, the breakpoint of 18.5°C is lower than others have reported. Hahn et al. (1992) reports a breakpoint of approximately 25°C. This discrepancy could also be related to lack of sufficient data points between 18 and 25°C.

Other studies indicate that there is a lag in thermoregulatory responses with respect to the environment (Gaughan et al. 2000; Hahn et al. 1997; Hahn 1999; Scott et al. 1983). These previous experiments have observed changes in lags during periods of evaluated temperature, thus lag time may provide important insights into thermoregulatory changes during heat stress. Except for the lag in t_{core} on days 1 and 2, the lags found in this study are consistent with those reported in the literature (Gaughan et al. 2000; Hahn et al. 1993, 1997). It is unclear at this time what would cause the extreme response observed in the lag of t_{core} on the first 2 days of the Columbia treatment.

Simulated heat-wave treatments were designed so that peak stress days were close to the middle of the treatment period (Columbia, days 8 and 9; Rockport, days 9 and 10). These peak stress days were determined by in field observations (Busby and Loy 1996; Hungerford et al. 2000; Mader et al. 2001). According to the literature, day 3 is the peak stress day for a cyclic heat stress treatment in many different species (Hahn 1999). Close examination of the metabolic changes over those peak stress days could provide some important insights into why those days in the field were so devastating.

The Cyclic treatment caused a peak in t_{core} and RR on day 3 of exposure, as expected. The increase in t_{core} over the first 3 days is a direct result of the animal not balancing its HP with its heat loss (Esmay and Dixon 1986). The increase in RR is a method of increasing heat loss, an attempt to balance the HP. Heat production decreases over these 3 days, therefore the increase in average t_{core} is due to a higher minimum t_{core} at the start of the day. This suggests that over this period (days 1–3) the animal cannot adequately cool itself during the nighttime or cool period of the day to offset the heat gains experienced during the peak heat period. During a heat-stress period, it has been found that cattle rely on cool nighttime temperatures to dissipate heat gained during the day (Bianca 1961; Kabuga 1991). Without sufficient cooling during nighttime hours, the animal's temperature would not return to normal levels, thus creating a higher peak in t_{core} the following day.

It appears between days 3 and 4 there is a metabolic shift in the animal that can be observed in many parameters. First, average RR and t_{core} start to decrease. There is a change in lags associated with RR and t_{core}, with respect to ambient temperature. On day 3, the lag in RR decreases (2.25–0.75 h) indicating that animals are adapting to thermal stress (Hahn 1989; Hahn et al. 1997). This is followed by an increase in lag in body temperature and ambient temperature on day 4 (3.75–7.75 h), suggesting that animal is able to compensate for heat gains over the first 3 days by over-cooling during night 4. This compensation on day 4 is partially due to a decrease in FI and a reduction in HP. During the first 3 days, FI decreases from 11.3±0.9 kg/animal on day 1 to 8.0±0.9 kg/animal on day 3, and then levels off with an average intake of 8.8±0.9 kg/animal. A decrease in FI would result in a decrease in HP (Close and Mount 1978; Esmay and Dixon 1986), which accounts for the decrease in HP over the first 3 days. However, HP continues to decrease until day 6, from 503.5±6.3 kJ/day/wt$^{0.75}$ (wt$^{0.75}$ is defined as metabolic body size), to 424.5±6.4 kJ/day/wt$^{0.75}$, and then remains fairly constant at an average of 436.8±6.4 kJ/day/wt$^{0.75}$. This continuing decrease of HP can be associated with a decrease in maintenance HP, which is caused by a decrease in organ sizes, resulting from the decrease in FI (Koong et al. 1985).

The ambient conditions in the Columbia treatment appear similar to the Cyclic treatment; however, the responses are somewhat different. The first 3 days of the Cyclic treatment both t_{core} and RR increased dramatically. In the Columbia treatment, while RR increases over the first 3 days t_{core} did not, indicating that at a slightly lower average ambient temperature the animals are able to dissipate heat produced by increasing RR. It appears that on days 3–7, average t_{core} is fairly constant and similar to days 5–11 in the Cyclic treatment, thus illustrating the animal's new balance point. The lag in RR is reasonably stable from days 2–7, also indicating homoeostasis. The lag in t_{core} is rather volatile over the first 7 days, which could be an indication that animals are changing their behavior (eating times, standing–laying patterns) to adapt to these higher temperature conditions. These animals appear to reduce their maintenance HP prior to the peak stress days, as illustrated on day 6 when FI increases, and HP continues to decrease. However, it is impossible to know the extent of this decrease. For this treatment, it appears that animals are not as severely stressed during peak stress days as animals exposed to the Cyclic treatment. During the peak stress period, the only indications of stress were an increase in t_{core} and a slight decrease in FI and HP; there is little or no change in RR, or the associated lags in RR or t_{core}. This indicates that the stress level in animals in the chamber are not equal to those in the field, with possible differences being wind speed and solar radiation, which are not simulated in the chamber study. This illustrates the importance of other environmental parameters, including wind speed and solar radiation, in determining stress level of the animals under field conditions.

The Rockport treatment is a very different pattern of heat stress than the other two heat stress treatments. The Rockport treatment had a few mild days, followed by a slow increase before the peak heat stress. The peak stress days (days 9 and 10) show some similar responses as the peak stress days of the Cyclic treatment. After the peak temperature on day 10, t_{core} and RR continue to increase through day 12, indicating a similar build up of heat as seen in the Cyclic treatment. This could be the result of a lack of acclimation to heat, which is a similar scenario as the Cyclic heat stress. The first sign of acclimation is observed on day 12, which happens to be the day RR and t_{core} peak. The lag associated with t_{core} appears to be very responsive to small changes in temperature, especially before the peak heat stress. A decrease in this lag is observed on the peak stress days (days 9 and 10), followed by an increase in lag time, as seen on day 4 of the Cyclic treatment. The lag associated with RR is consistent through day 9, followed by an increase in lag time on days 10–12, which was quite different than the observations for the Cyclic temperature. In summary, it appears that the conditions at Rockport, Mo. are devastating because of the rapid onset of critically hot conditions, and possibly the animals are not sufficiently acclimated to hot weather.

Conclusions

Respiration rate was affected mostly by ambient temperature, with little variation in response left unaccounted. Animal and temperature equally affected the variation in t_{core}. Feed intake and HP were the only parameters to have a significant quadratic effect. Temperature (using both linear and quadratic components) explained only 32% of the variation in FI. Using both linear and quadratic terms, temperature explained 56% of the variation in HP; the quadratic term accounted for a large portion of the variation. No animal effect could be evaluated because HP was measured on a chamber basis (three animals).

It appears that RR has some unique qualities that make it a useful stress indicator. First, it is responsive to ambient temperature, and unlike t_{core}, individual animal accounts for only a small percentage of the total variation. Second, the lag associated with RR and ambient temperature was reasonably constant (0–4.5 h), and was similar in animals exposed to thermoneutral and heat stress conditions (unlike the lag associated with t_{core}, which varied from 3 to 13.5 h, and was 1.6 h shorter under heat stress conditions compared to thermoneutral conditions). Finally, respiration rate is an easy parameter for producers to measure, without the need for additional equipment.

It appears that the Cyclic heat-stress treatment is a representative model to test the thermoregulatory responses of cattle. This treatment provided some insights into an acute heat-stress event, like the one at Rockport, Mo.. Based on these results, the heat wave centered around Rockport, Mo., in July 1999 was devastating because the animals were not acclimated to extreme heat. However, it appears that the Cyclic treatment does not accurately reflect semi-acclimated cattle, like those at Columbia, Mo., in 1999. The responses of the cattle to conditions at Columbia, Mo. showed some acclimation to heat prior to the peak stress days, and therefore a dampened response was seen. Apparently, the extreme conditions at Columbia, Mo., in 1999 were made severe by environmental conditions not simulated during this study (low wind speed and intensive solar radiation). While environmental chambers offer precise control of environmental conditions, they lack the solar radiation, wind speed, and animal interaction of a natural environment. These results illustrate the need to complete similar studies in feedlot settings.

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